

# Cyclic competition of four species: domains and interfaces

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**Abstract.** We study numerically domain growth and interface fluctuations in one- and two-dimensional lattice systems composed of four species that interact in a cyclic way. Particle mobility is implemented through exchanges of particles located on neighboring lattice sites. For the chain we find that the details of the domain growth strongly depend on the mobility, with a higher mobility yielding a larger effective domain growth exponent. In two space dimensions, when also exchanges between mutually neutral particles are possible, both domain growth and interface fluctuations display universal regimes that are independent of the predation and exchange rates.

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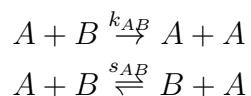
## 1. Introduction

Since the seminal works of Lotka [1] and Volterra [2], many in-depth studies of model systems yielded important insights into food webs and other ecological systems. Using the methods of non-linear and statistical physics, these investigations allowed to make notable progress in our understanding of biodiversity, species coexistence, and species extinction [3, 4, 5, 6, 7]. Recent years saw a flurry of studies of systems composed of multiple species that interact in a cyclic way. Most of these studies focused on the case of three species [8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 31, 32, 33, 34, 35, 36, 37, 38, 39], a special situation where every species interact with every other species. Only rather few papers, however, dealt with more realistic cases where a given species interacts with only a subgroup of all species living in the same ecological environment [6, 8, 9, 29, 40, 41, 42, 43, 44, 45, 46, 47, 48, 50, 51, 52, 53, 54, 55, 56].

The case of four species interacting in a cyclic way is characterized by the formation of two alliances of neutral species, i.e. species that are not in a predator-prey relationship. In the well-mixed situation [51, 52, 55] a variety of orbits in configuration space are obtained in mean field approximation. Stochastic evolution of finite systems shows a good agreement with the mean field results, but also reveals interesting additional aspects, most notably those related to various extinction scenarios. Restricting themselves to predation events, Frachebourg *et al.* [8, 9] studied one-dimensional coarsening and the related algebraic domain growth. Segregation and the formation of defensive alliances in two dimensions have been studied in [41, 44, 45, 46, 47, 48] for a variety of interaction schemes and/or different realizations of particle mobility.

The studies of cyclically competing species have allowed to address a variety of problems, ranging from biodiversity and species extinction to the formation of space-time pattern. In the present work we address generic properties of pattern formation during a coarsening process that involves multiple species. For this we study domain growth and interface fluctuations in one- and two-dimensional lattice systems when four species compete cyclically.

Calling the four species  $A$ ,  $B$ ,  $C$ , and  $D$ , we prepare fully occupied lattices of  $N$  sites by placing for each of the four species particles on  $N/4$  randomly selected lattice sites. Here  $A$  is the predator of  $B$ , whereas  $B$  preys on  $C$ ,  $C$  on  $D$ , and  $D$  on  $A$ . We update the system by randomly selecting a pair of neighboring sites. If the individuals on the selected two sites are in a predator-prey relationship, then one of the following three events can occur: predation takes place where the prey is replaced by a predator, the two individuals swap places, or nothing happens. This can be written in the following way:



and so on. Here,  $k_{AB}$  and  $s_{AB}$  are the predation and swapping rates between an  $A$  and a  $B$  particle, with  $k_{AB} + s_{AB} \leq 1$ . If, on the other hand, the two selected individuals are neutral, as it is the case for  $A$  and  $C$  particles, for example, then they can exchange places with rate  $s_n$  [47]. The results for domain growth and interface fluctuations discussed in the following have been obtained for cases where all the predation rates are identical,  $k = k_{AB} = k_{BC} = k_{CD} = k_{DA}$ . In addition, we also set all the swapping rates between predator-prey pairs to be equal,  $s = s_{AB} = s_{BC} = s_{CD} = s_{DA}$ . In this way, we avoid having a bias in favor of one of the alliances.

The remainder of the paper is organized in the following way. In the next Section we discuss the impact of mobility on the coarsening process in one dimension. When exchanges between neutral particles are forbidden, an effective algebraic growth law is encountered where the exponent increases with increasing swapping rate. If we also allow for exchanges between neutral pairs, the domains grow exponentially fast. The two-dimensional case is the subject of Section 3. For that case we also find that adding swappings between neutral pairs changes qualitatively the domain growth. Indeed, in case of identical predation and exchange rates for all predator-prey pairs, the system ends up in a steady state where all species coexist. However, when we allow for exchanges between neutral pairs, coarsening sets in where the domains only contain mutually neutral partners. In variance with the one-dimensional case the exponent of the algebraic growth in two dimensions is found to be independent of the values  $k$  and  $s$  of the predation and swapping rates. Section 4 focuses on the interface fluctuations between domains composed of partner-pairs. We thereby find that the interface fluctuations belong to the Edwards-Wilkinson universality class [57]. Finally, in Section 5 we discuss our findings and conclude.

## 2. Coarsening in one dimension

In low dimensions stochastic effects have a remarkable impact on the properties of non-equilibrium systems, as evidenced for example by the non-trivial nature of many non-equilibrium phase transitions taking place in one dimension [58]. Coarsening processes in one dimension are usually substantially different from those taking place at higher dimensions. In a series of papers Frachebourg *et al.* [8, 9, 42] studied the coarsening process in one-dimensional systems composed of multiple species that interact in a cyclic way. Restricting themselves to immobile particles, they found algebraically growing domains both for three and four species, but with different values of the growth exponent:  $3/4$  for three species and  $1/3$  for four species. For larger numbers of species, the system rapidly settles into a blocked configuration where neighboring pairs are non-interacting.

Recent studies of three species systems have shown the importance of particle mobility when cyclic dominance prevails [15, 18, 16, 21]. Thus in two dimensions mobility induces qualitative changes in cases where the total number of particles is not conserved. Whereas for low mobility biodiversity prevails, medium values of the mobility lead to species extinction. Further increasing the mobility finally yields an enhanced

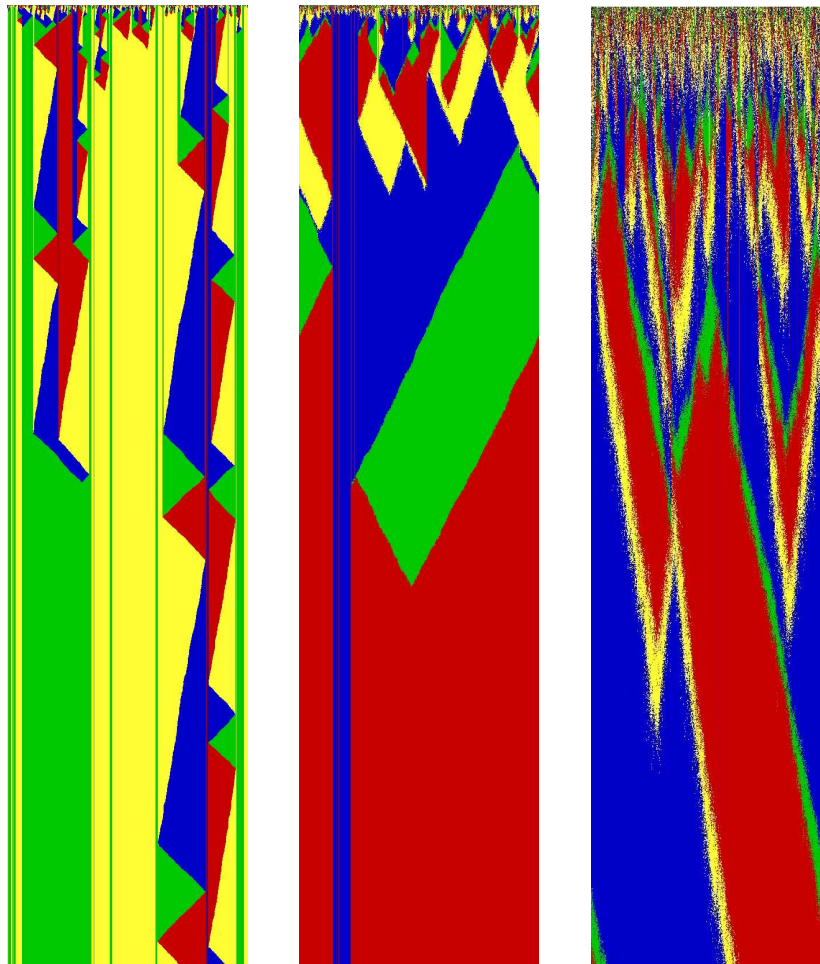
mixing paired with the (re)emergence of species coexistence. In one dimension one finds for the case of conserved particle number that coarsening takes place at low mobility, paired with a power-law increase of the average domain size. For high swapping rates, however, complex space-time patterns emerge that ultimately yield a non-equilibrium steady state where all three species coexist.

In order to get a first impression on how mobility changes one-dimensional coarsening for four species we can have a look at the space-time diagrams shown in Figure 1. These diagrams have been obtained for small systems composed of  $N = 2500$  sites, with periodic boundary conditions. As usual, time is measured in Monte Carlo Steps (MCS), with one MCS corresponding to  $N$  proposed updates. In all three cases shown in that figure, we have set  $k + s = 1$ . The left diagram shows the typical time evolution of the system for small swapping rates. As for the case without swapping [9] we see rapidly the emergence of partner-pair domains (green and yellow versus red and blue) that are very stable against attacks of the competing alliance. Consider for example the case where a yellow and a blue domain are in contact. As the  $B$  particles (yellow) are the preys of the  $A$  particles (blue), the blue domain expands into the yellow domain until this front meets some  $D$  particles (green domains). Now, the roles are changed, and the blue domain decreases as the  $A$  particles are replaced by  $D$  particles. This continues until the expanding green domain encounters a red domain, and so on. This rather complicated coarsening process keeps going on until only one alliance fills the complete system. Increasing the swapping rate leaves this scenario unchanged (see middle diagram), but coarsening seems to proceed in an accelerated way. Indeed, a higher swapping rate allows the prey to survive with a finite probability the passage through small domains of its predators, so that the protection due to the pairing of neutral partners becomes less effective. For very high swapping rate, see the right diagram, it takes some time before first domains form. Once these domains are formed, the coarsening proceeds very rapidly.

This discussion can be made more quantitative by looking at the average domain size,  $\langle \lambda \rangle$ , see Figure 2, for various cases with  $k + s = 1$ . We thereby define as average domain size the average length of the segments composed by only one species. For small swapping rates the domain growth proceeds as for the immobile case, yielding an algebraic relationship  $\langle \lambda \rangle \sim t^\delta$ , where  $\delta = 1/3$  is the exactly known value when  $s = 0$  [9], see the dashed line. Increasing the value of  $s$  has two notable effects. First, the increase at early times gets slower and slower, thus revealing that the enhanced mobility makes it more difficult for the initial domains to form. Once ordered segments have formed, however, the growth proceeds much faster than for the  $s = 0$  case. In order to see that we show in the inset the time dependence of the effective exponent

$$\delta_{eff}(t) = [\ln(\langle \lambda \rangle(10t)) - \ln(\langle \lambda \rangle(t))] / [\ln(10t) - \ln(t)] . \quad (1)$$

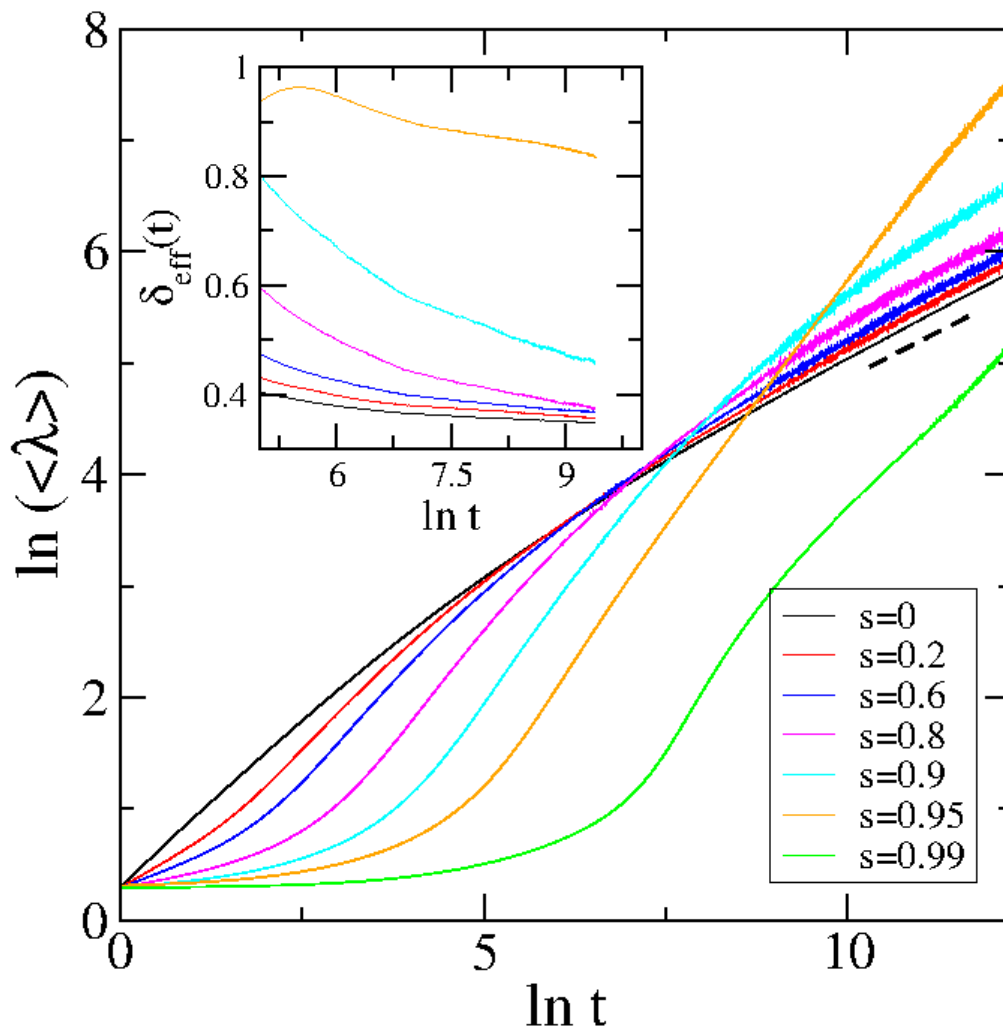
We see that this time-dependent effective exponent decreases for increasing times. In fact, the existing data leave open the possibility that asymptotically the value  $1/3$  is recovered for extremely long times.



**Figure 1.** Space-time diagrams (time increases from top to bottom) for one-dimensional systems with three different predation and exchange rates:  $k = 0.8$ ,  $s = 0.2$ ,  $s_n = 0$  (left),  $k = 0.1$ ,  $s = 0.9$ ,  $s_n = 0$  (middle),  $k = 0.01$ ,  $s = 0.99$ ,  $s_n = 0$  (right). The system size is  $N = 2500$ , the total simulation time is  $t_{max} = 10000$  MCS. Periodic boundary conditions are used. Blue:  $A$  particles, yellow:  $B$  particles, red:  $C$  particles, green:  $D$  particles.

This behavior, which is due to the formation of neutral alliances, is very different to what is observed in the three species case, see Figures 1 and 2 in [21]. Indeed, as in the three species case every species interact with every other, one does not have regions formed by domains of mutually neutral species. As a result increasing the swapping rate in that case does not yield an acceleration of the coarsening, and the domain growth exponent remains unchanged. It is only for very large swapping rates that a notable change sets in, yielding a non-equilibrium steady state with constant average domain size, as the system is then well mixed [21]. We expect the scenario observed in the present paper for the four species case to be very generic for systems with cyclic dominance composed of multiple species, as long as different species can form neutral alliances to fight off their predators.

Following [47] we can also allow for exchanges between neutral pairs, i.e. swappings

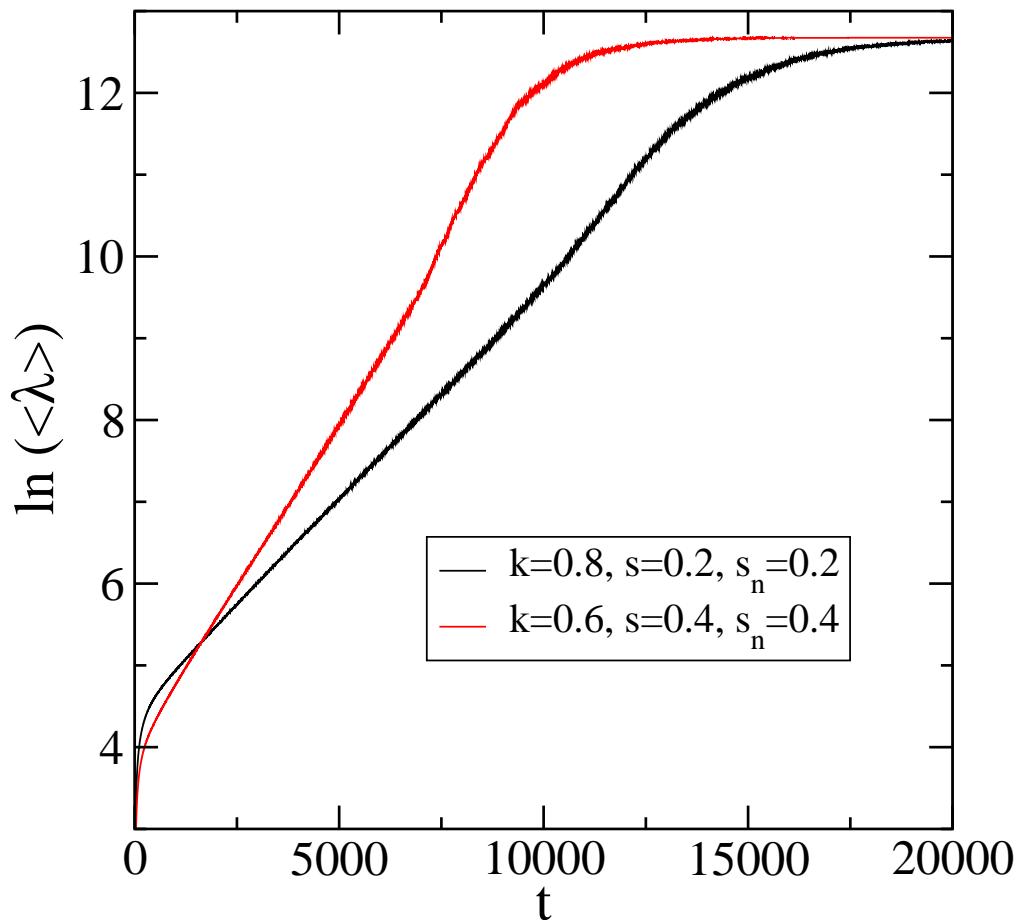


**Figure 2.** Average domain size as a function of time for different swapping rates  $s$ , with  $k + s = 1$ . The systems contain 36000 lattice sites. The dashed line indicates the exponent  $1/3$  known exactly for the case of immobile particles. The inset shows the time-dependence of the effective exponent (1). The shown data have been obtained after averaging over typically 3000 different realizations of the noise.

of neighboring  $A$  and  $C$  particles or  $B$  and  $D$  particles with rate  $s_n$ . In that case we observe, see Figure 3, that the domain growth proceeds in an explosive way, yielding a typical domain size that increases exponentially with time. Obviously, exchanges between neutral partners weakens the lines of defense that result from alternating domains formed by the partners, see Figure 1, which drastically increases the probability of dissolving smaller domains.

### 3. Coarsening in two dimensions

A variety of studies have clarified some of the properties encountered when putting  $M > 3$  species with cyclic dominance on a square lattice. Early on Frachebourg and Krapivsky [42] found that in the absence of particle mobility systems with more than 14



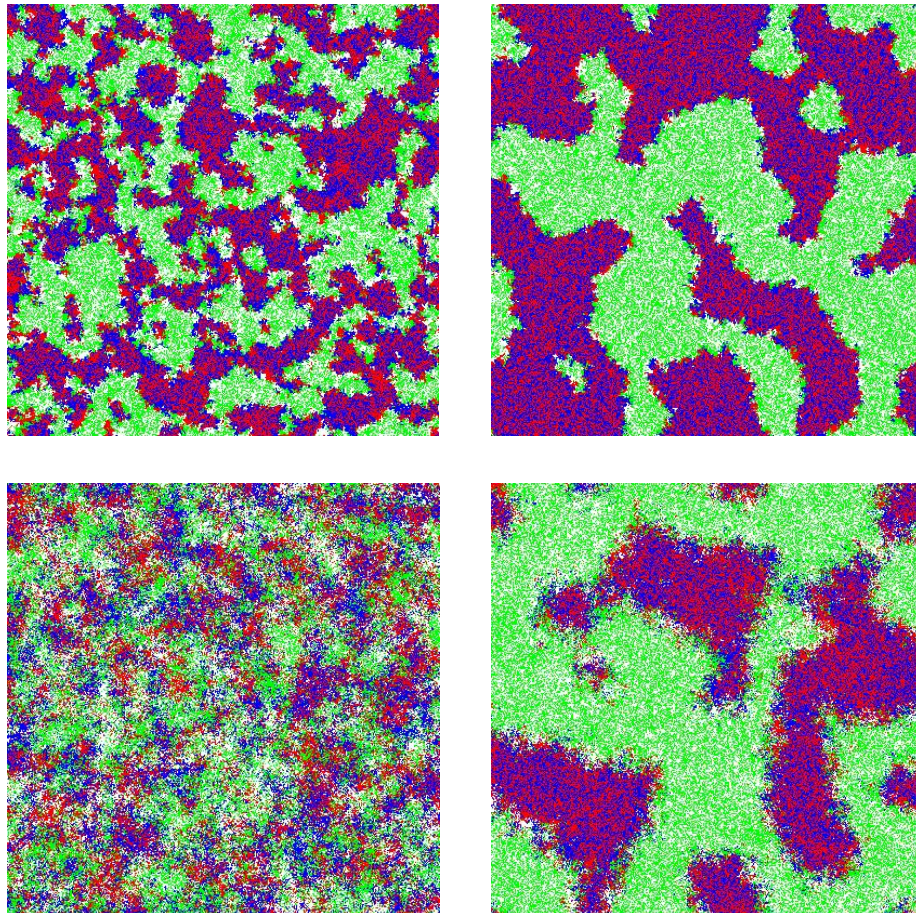
**Figure 3.** Allowing for swapping between neutral pairs yields an exponential increase of the domain size, as shown in this linear-log plot. Systems with 36000 sites are considered.

species end up in a frozen state where all particles are surrounded by neutral partners. For the case we are interested in, namely that of four species, the system settles into a steady state where all four species coexist. Allowing for mobile particles through the diffusion via unoccupied sites yields a qualitative change [45]. For small densities of empty sites the behavior is similar to that of immobile particles, and all four species coexist. For higher densities, however, a coarsening regime is revealed where partner-pairs are competing against each other, yielding the formation of domains that contain only neutral species. A similar transition between a regime of species coexistence and a regime where species extinction proceeds through a coarsening process is observed for a completely filled lattice when exchanges between neutral partners take place [47]. No exchanges between predators and preys were allowed in that work.

In the following we study the coarsening process taking place in our system when exchanges between neutral partners are allowed in addition to interactions (predation and exchange) between predators and preys. We thereby focus on two different sets of rates, namely (1)  $k = 0.8$  and  $s = s_n = 0.2$  and (2)  $k = 0.2$  and  $s = s_n = 0.8$ , similar results being obtained for other values of predation and swapping rates. We stress



that, in agreement with [47], coarsening does not take place in absence of exchanges between neutral partners, but instead the system then ends up in a stationary state with coexistence.

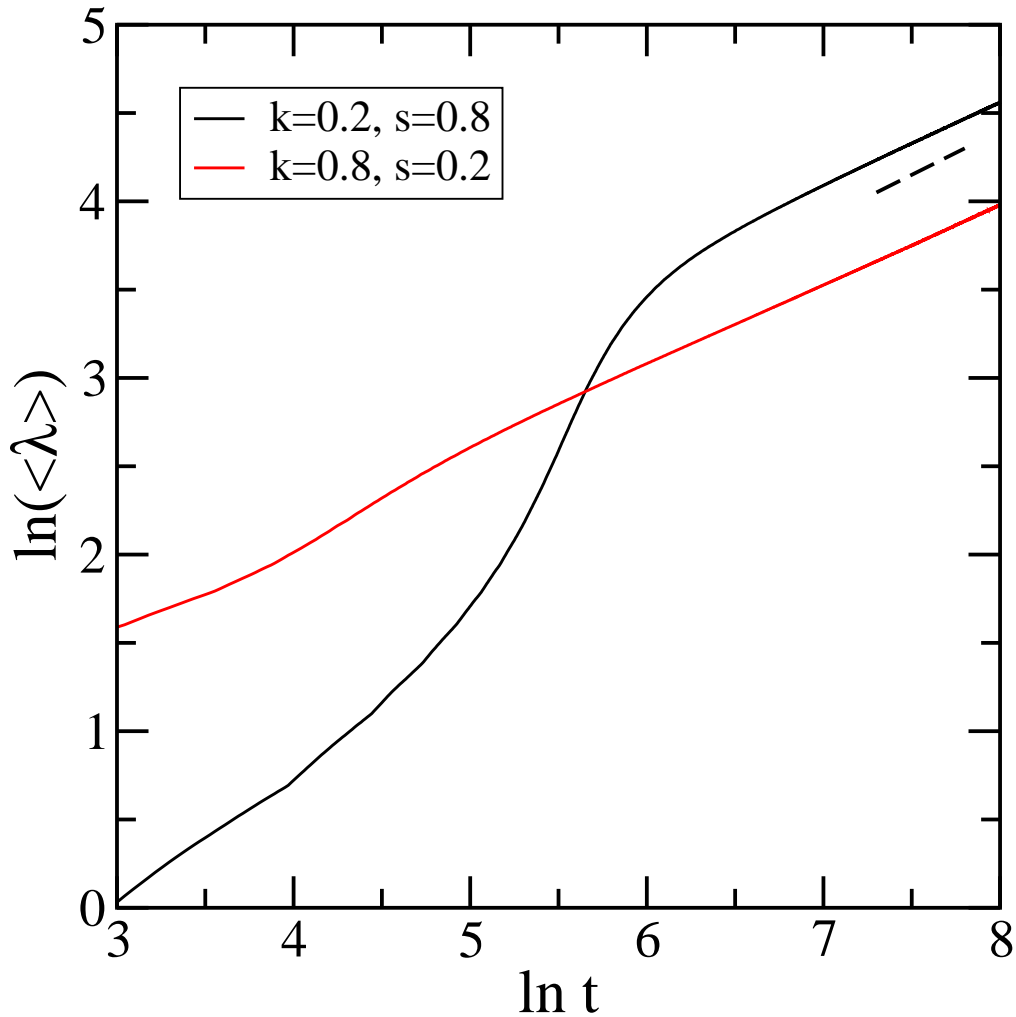


**Figure 4.** Configurations during coarsening in two dimensions. Top row:  $k = 0.8$  and  $s = s_n = 0.2$ , bottom row:  $k = 0.2$  and  $s = s_n = 0.8$ . The left column shows the systems 100 MCS after initialization, the snapshots in the right column are taken after 500 MCS. The system size is  $400 \times 400$ , and periodic boundary conditions are used.

Let us again start by having a look at some configurations, see Figure 4, where the two different cases are displayed. The first row shows two snapshots, one after 100 MCS and one after 500 MCS, for  $k = 0.8$  and  $s = s_n = 0.2$ . As expected, one observes the formation of domains that are composed of mutually neutral species, namely  $A$  and  $C$  (blue and red) or  $B$  and  $D$  (white and green). These domains then coarsen until, eventually, only one alliance will prevail in our finite system. For the case  $k = 0.2$  and  $s = s_n = 0.8$ , shown in the second row, domains are not yet well formed after 100 MCS. At a later time we again have coarsening, where smaller domains give place to larger domains, but the boundaries of the domains are very fuzzy. These effects are of course due to the enhanced swapping rate and are similar to those observed in the one-dimensional case, see Figure 1.

Due to the fact that the boundaries of the domains are not very sharp, we determine





**Figure 5.** Average correlation length as a function of time for the same two sets of predation and exchange rates as those used in Figure 4. The dashed line indicates the slope  $1/2$ . The system size is  $800 \times 800$ , and the data result from an average over 8000 independent runs.

the typical length in our system through a study of the correlation function,

$$C(t, \mathbf{r}) = \sum_i [\langle n_i(t, \mathbf{r}) n_i(0, \mathbf{0}) \rangle - \langle n_i(t, \mathbf{r}) \rangle \langle n_i(0, \mathbf{0}) \rangle] . \quad (2)$$

Here  $n_i(t, \mathbf{r})$  is an occupation number that is 1 when at time  $t$  site  $\mathbf{r}$  is occupied by a particle of species  $i$  and 0 otherwise.  $\langle \dots \rangle$  indicates an average over initial states and over the realizations of the noise. We then define the correlation length  $\lambda(t)$  as the distance at which  $C(t, \mathbf{r})$  drops to one third of the value it has at  $\mathbf{r} = \mathbf{0}$ . The result of this analysis is shown in Figure 5. At short times the correlation length is much smaller for the larger swapping rate, see the black line in the figure, in accordance with our observation that in that case it takes longer for domains to form. Once these domains are formed, the coarsening undergoes a regime of rapid growth before entering the asymptotic regime. This behavior is in fact very similar to what happens in the  $d = 1$  case, see Figure 2. However, whereas in one dimension the asymptotic regime is characterized by an

algebraic growth with mobility dependent exponents, in two dimensions the asymptotic growth is the same for the studied cases, with  $\langle \lambda(t) \rangle \sim t^{1/2}$ . This universal exponent  $1/2$ , which has also been observed in other variants of the four species model on the square lattice [6], is expected from the Allen-Cahn law for curvature-driven coarsening [59, 60, 61].

#### 4. Interface fluctuations

Even so the same growth law prevails in two dimensions for different reaction rates, the boundaries between the different domains can look very differently, see the configurations shown in Figure 4. Whereas for small swapping rates these boundaries are very sharp, they get increasingly fuzzier when increasing this exchange rate. It is therefore *a priori* not clear that interfaces for different rates have the same properties.

In order to elucidate this we prepare our system such that in one half we have only  $A$  and  $C$  particles, whereas the other half is formed by the competing alliance composed of  $B$  and  $D$  particles. We start with a sharp, straight interface, using reflective boundaries in the direction perpendicular to the interface and periodic boundary conditions parallel to the interface. We then update the system using the same rules as before and monitor the roughening of the interface, see Figure 6 for two examples.

Interface fluctuations are usually studied in a quantitative way through the interface width. For large swapping rates, however, the interface is very diffuse, due to the many exchanges taking place at the boundaries between the two alliances. In order to determine the local position of the interface, we assign the value  $+1$  to every  $A$  and  $C$  particle and the value  $-1$  to every  $B$  and  $D$  particle and then proceed as in [62] (see also [63]). Considering rectangular systems of  $L \times H$  spins, we determine for each row  $j$  the value  $\ell$  that minimizes the sum

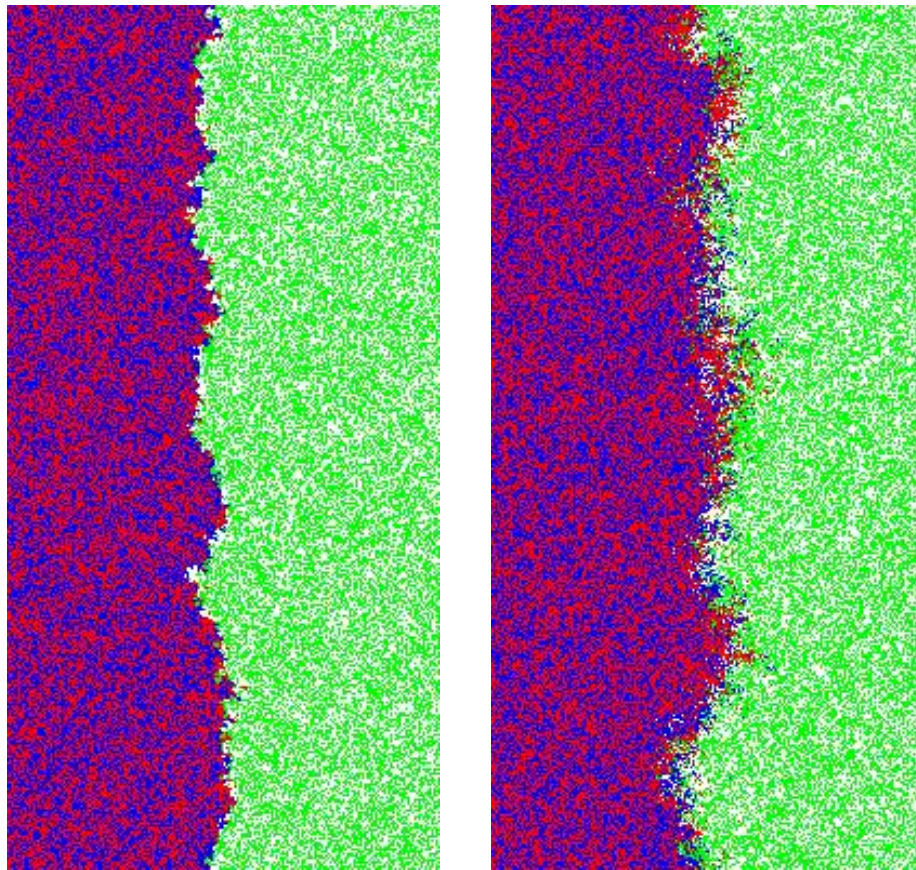
$$v(\ell) = \sum_{i=1}^L [S_{i,j} - p(i - \ell)]^2 . \quad (3)$$

Here,  $S_{i,j} = \pm 1$ , depending on which alliance occupies site  $(i, j)$ , and  $p(u)$  is a step function, with  $p = 1$  for  $u < 0$  and  $p = -1$  for  $u > 0$  [62]. The local position of the interface at row  $j$ ,  $\ell(j)$ , is then given by the value of  $\ell$  that minimizes (3). With this coarse-grained interface profile at hand, we compute the time-dependent interface width

$$W(t) = \sqrt{\frac{1}{H} \sum_{j=1}^H (\ell(j) - \bar{\ell})^2} , \quad (4)$$

where  $\bar{\ell} = \frac{1}{H} \sum_{j=1}^H \ell(j)$  is the mean position of the fluctuating interface at time  $t$ .

Figure 7 shows the time evolution of the interface width for the case  $k = 0.8$ ,  $s = 0.2$ , and  $s_n = 0.2$ . We observe three different regimes, as expected for the width of an interface that initially was given by a straight line: uncorrelated fluctuations prevail at early times, followed by a correlated fluctuation regime, before the fluctuations saturate



**Figure 6.** Snapshots of two systems where each half of the system is initially occupied by one alliance. Left:  $k = 0.5$ ,  $s = 0.5$ , and  $s_n = 0.5$ ; right:  $k = 0.2$ ,  $s = 0.8$ , and  $s_n = 0.8$ . The system size is  $200 \times 400$ , the configurations are obtained after 980 MCS.

at a level that depends on the length  $H$  of the interface. The two last regimes can be summarized by the Family-Vicsek scaling relation [64, 65]

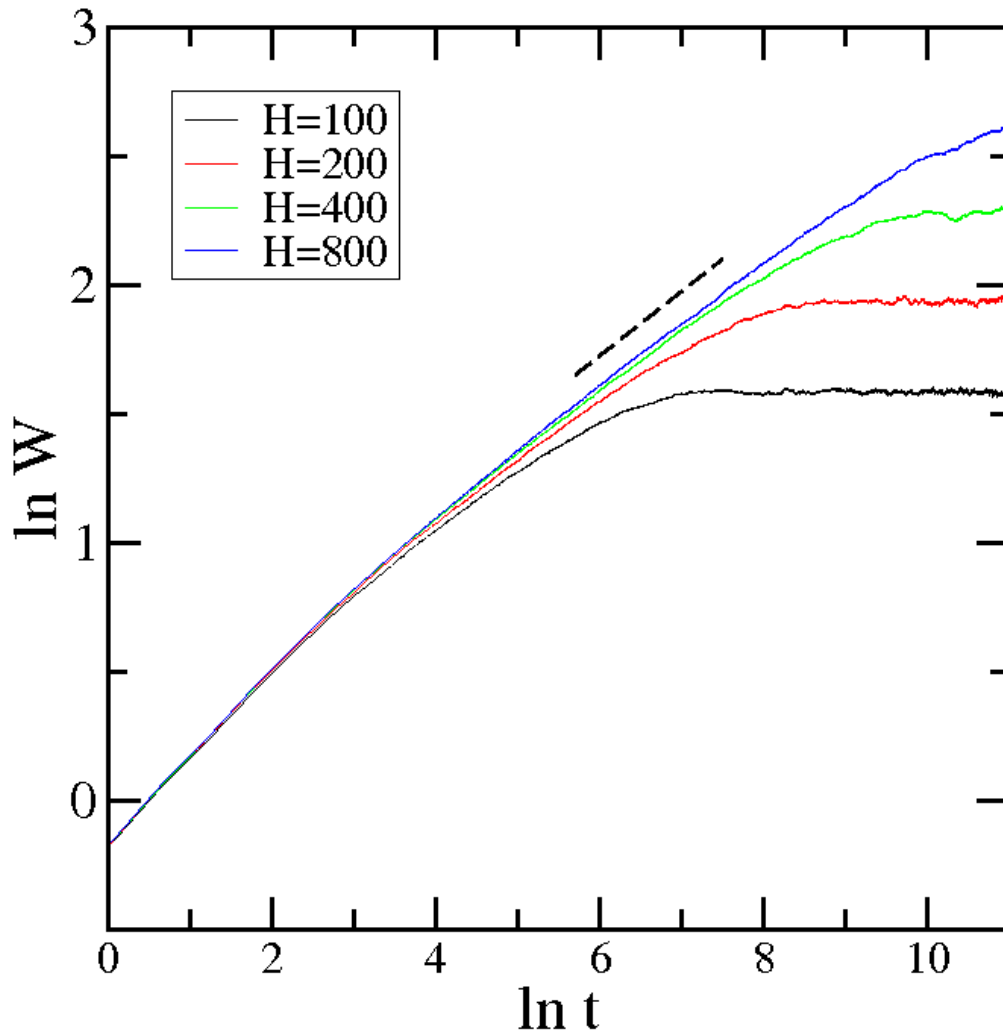
$$W(t, H) = H^\alpha f(t/H^{\alpha/\beta}) , \quad (5)$$

with the growth exponent  $\beta$  and the roughness exponent  $\alpha$ . It follows from this relation that the width should grow as  $t^\beta$  in the correlated regime and that the value of saturation should scale as  $H^\alpha$  with the interface length. Analyzing our data, we find in the two studied cases that  $\beta = 1/4$  (this is indicated by the dashed line in Figure 7) and  $\alpha = 1/2$ , in agreement with the values expected for the Edwards-Wilkinson universality class [57].

## 5. Conclusion

When four species compete cyclically, the formation of two alliances of mutually neutral partners is observed. As a result, species extinction, when it takes place, proceeds through a coarsening process where domains formed by the different alliances expand until one alliance fills the whole system.

In this work we studied the properties of this coarsening process, both in one and two dimensions. It is known from earlier studies [8, 9] that in the case of immobile



**Figure 7.** Time evolution of the interface width for the case  $k = 0.8$ ,  $s = 0.2$ , and  $s_n = 0.2$ . Rectangular systems with  $L \times H$  sites are considered, where  $L = 200$ . The dashed line indicates the expected power law for correlated fluctuations belonging to the Edwards-Wilkinson universality class. The data result from averaging over at least 2000 independent realizations of the noise.

particles the four species form domains in one dimension that grow algebraically in time with an exponent  $1/3$ . Mobile particles render the formation of initial domains more difficult. Once these domains are formed, however, the growth proceeds very fast. If only predator-prey pairs are allowed to exchange sites, then we obtain an effective power law exponent whose value increases with the swapping rate. If in addition neutral pairs can swap places, then the domains grow exponentially fast. In two dimensions the system settles in a steady state characterized by the coexistence of all four species if no exchanges between neutral partners take place. Allowing for these exchanges, though, yields the formation of domains formed by partner-pairs, followed by a coarsening process. Even so the boundaries between the domains can change their character, being sharp for small exchange rates, but fuzzy for larger rates, the domain growth exponent takes on

the value  $1/2$ , as expected for curvature-driven coarsening. In addition, after coarse-graining the interface, we find that the interface fluctuations are characterized by the exponents of the Edwards-Wilkinson universality class.

Obviously, the properties of four species that interact in a cyclic way are very different from those encountered for the case of three species. Three species form in fact a very special situation, as here every species interact with every other species. In four and more species, however, there are mutually neutral species. As a consequence one observes for an even number of species the formation of alliances of non-interacting species, thereby enhancing the efficiency of the different species to fight off their predators. As this is a very general mechanism, we expect our results for four species to be representative also for other systems, as long as the species can arrange themselves in two alliances composed exclusively by partners that are mutually neutral.

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